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LARVAL SETTLEMENT OF A SYMBIOTIC HYDROID: SPECIFICITY AND NEMATOCYST RESPONSES IN PLANULAE OF *PROBOSCIDACTYLA FLAVICIRRATA*

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Planktonic larvae of many benthic invertebrates preferentially settle and metamorphose on specific substrates (Williams, 1964; Newell, 1970). Frequently, the planktonic larvae of symbionts possess exceptionally well-developed physiological mechanisms for substrate selection. Such mechanisms presumably evolved because, for these species, only a small proportion of the surfaces that a larva might contact are suitable for settlement (Davenport, 1955). I have studied planulae of the symbiotic hydroid *Proboscidactyla flavicirrata* (Brant). The structure of a planula larva is extremely simple, yet the planulae of *Proboscidactyla* settle with great specificity (Campbell, 1968).

Sabellid polychaetes are the only known hosts of *Proboscidactyla* (Gosse, 1857; Uchida and Okuda, 1941; Hand, 1954; Brinkmann and Vannucci, 1965; Calder, 1970). *Proboscidactyla* colonies are found on the rims of sabellid tubes where their gastrozooids can contact the host's plume of tentacular cirri. According to Campbell (1968), *Proboscidactyla* planulae begin settlement by adhering with nematocysts to the pinnules that branch from the tentacular cirri. Later, when the sabellid retracts its tentacular cirri into its tube, the planulae somehow transfer to the rim of the tube where they metamorphose.

In this report I confirm and extend Campbell's work. Two new findings are of particular importance. First, planulae use nematocysts both to attach to pinnules as Campbell (1968) suggested and to transfer to the tube rim. Between the time of attachment to a pinnule and transfer to the tube rim, the effective stimulus for nematocyst discharge shifts from pinnule to worm tube. Secondly, planulae settle and metamorphose on either of two sympatric species of sabellids, one of which does not support *Proboscidactyla* colonies.

MATERIALS AND METHODS

During June, July, and August of 1973, the medusae of *Proboscidactyla* were collected from surface waters, and the sabellids *Schizobranchia insignis* and *Eudistylia vancouveri* from the undersides of mooring floats near the University of Washington Friday Harbor Laboratories. Nearly mature *Proboscidatyla* medusae sometimes ripened when fed *Artemia* larvae. The medusae, embryos, and planulae were kept in glass finger bowls or Syracuse dishes partially submerged in an open-circulation sea table and the water in the holding containers was changed at least every third day.

The medusae shed their gametes at night and developing embryos were routinely transferred to Syracuse dishes the next morning. Zygotes were sometimes collected during the night to examine early development. Individual planulae, severed sabellid pinnules, and fragments of sabellid tubes were handled using tygon suction micropipettes (Josephson, 1965) held in micromanipulators.

The micrographs illustrating this report were made with incident illumination using either a Wild M-5 stereo microscope, or a Zeiss photomicroscope equipped with Nomarski differential interference contrast optics.

RESULTS

Development

Cleavage in *Proboscidactyla* eggs was holoblastic, unilateral, and equal or nearly equal. Cleavages 2 through 7 occurred at approximately 45 min intervals (14° C). A blastula had formed by 6 hr after fertilization. After about 10 hr individual blastomeres began to migrate inward to form the entoderm. In the majority of the embryos this migratory activity was basically unipolar, although small groups of cells sometimes ingressed away from the main site of gastrulation. In a few embryos, migratory cells were distributed almost uniformly over the inner surfaces of gastrulae. Nevertheless, as gastrulation progressed, the entoderm always thickened toward the pole that eventually became the posterior end of the swimming planula (see Fig. 1).

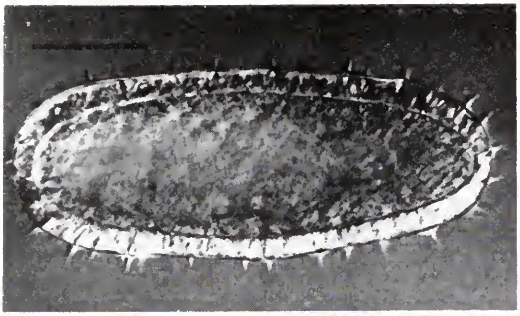
Cilia first appeared 14 hr after fertilization and at about 16 hr the planulae began to crawl and swim. At approximately the same time the planulae started to change shape, alternately becoming ovoid and nearly spherical. Planulae swam and crawled only when in the ovoid shape. Those crawling along the bottoms of dishes advanced without rotating, but swimming planulae always rotated slowly on their long axes in a clockwise direction when viewed from the anterior end. According to Widerstein (1968) such clockwise rotation is a common feature in cnidarian larvae.

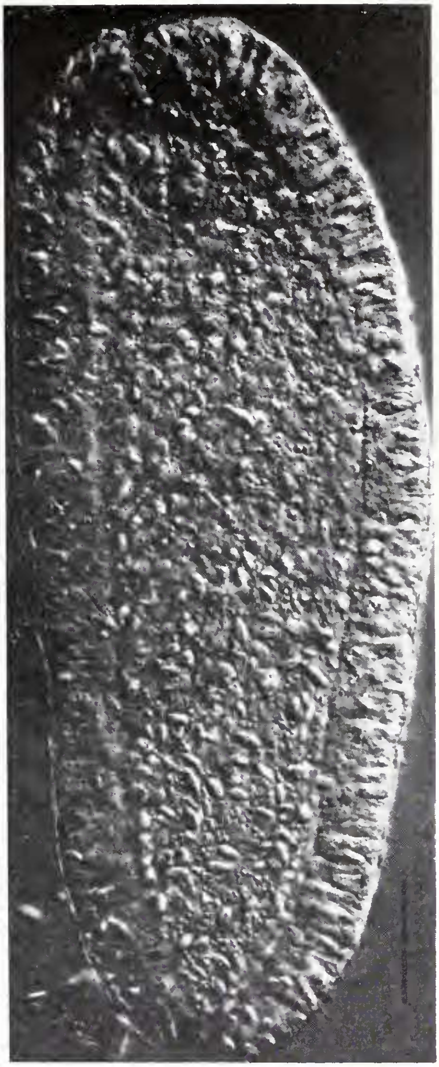
The Cnidome

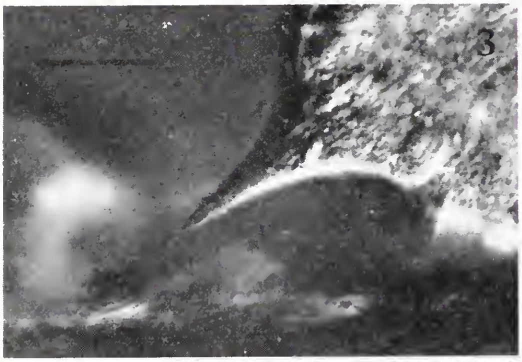
Cnidocils began to protrude from the epidermis about 48 hr after fertilization. During the 24 hr that followed, their numbers gradually increased, presumably as more and more nematocysts matured or reached peripheral locations. During this period of development the planulae were periodically touched with severed *Schizobranchia* pinnules to determine whether they had acquired the ability to attach.

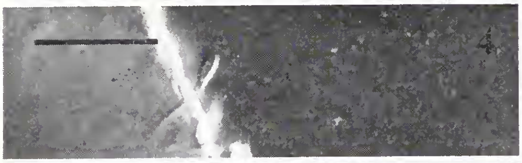
Prior to the appearance of cnidocils about 36 hr after fertilization, planulae never adhered to pinnules even momentarily. About 48 hr after fertilization, while the cnidocils were still comparatively sparse, planulae sometimes adhered but failed to remain attached for more than a few seconds. After 72 hr the density of cnidocils on the surface appeared to have reached its maximum. Planulae that touched *Schizobranchia* pinnules more than 72 hr after fertilization always attached and usually remained attached even if jostled vigorously.

Peripheral nematocysts in fully developed planulae were distributed almost uniformly over the ectoderm (Fig. 1). No concentration of nematocysts in the ectoderm of the anterior end comparable to that reported by Campbell (1968) was









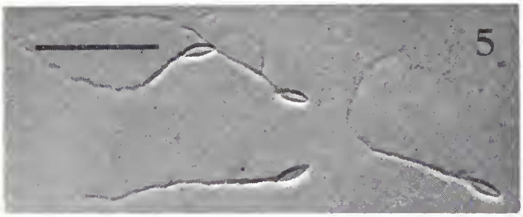


FIGURE 1. Protruding cnidocils distributed fairly uniformly in the epidermis of a fully developed planula. The cavity within the planula appears as a lighter area centered nearer the anterior end (left). The entoderm is correspondingly thicker toward the posterior end; scale bar = 50 μ.

FIGURE 2. Optical section of a planula showing a concentration of nematocyst capsules in the posterior entoderm (bottom third). (Fig. 2–5 are all to the same scale and the nematocyst capsules depicted in these figures all appear similar); scale bar = 25 μ.

FIGURE 3. Epidermal distortion formed by pulling an adhering planula away from a fragment of sabellid tube; scale bar = 25 μ.

FIGURE 4. Nematocyst discharged into a fragment of sabellid tube. A portion of the embedded thread can be seen leading down and left from the capsule; scale bar = 25 μ.

FIGURE 5. Discharge epidermal nematocysts; scale bar = 25 μ.

apparent. Nematocyst capsules were present in the entoderm as well, mainly toward the posterior end where the entoderm was thickest (Fig. 2).

Mechanism of adhesion

In nature, a *Proboscidactyla* planula contacts 2 different substrates during the course of settlement. Initially it adheres to a sabellid pinnule (attachment). While still attached to the pinnule it adheres to the rim of the sabellid's tube (the initial event in transfer). The simultaneous acquisition of cnidocils and attachment capability suggested that nematocysts are responsible for adhesion to pinnules. This was comfirmed by pulling attached planulae off pinnules with micromanipulators. As planula and pinnule separated, areas of the planula epidermis stretched into cones attached to the pinnule at their apices (Fig. 3). At each apex was a discharged nematocyst with its thread embedded in the pinnule. Similar experiments performed with planulae that had transferred from pinnules to fragments of sabellid tube produced identical results. Nematocyst capsules left upon pinnules and tube fragments were also observed after planulae had been dislodged from their sites of adhesion. If the site was the edge of a thin piece of tube the embedded thread could sometimes be seen as well as the capsule (Fig. 4). Although each planula possessed over a hundred epidermal nematocysts, only a few (usually less than 5) were discharged during an adhesion. This suggested that nematocysts of planulae do not discharge unless the corresponding cnidocils contact sabellid surfaces.

Planulae released both everted and undischarged nematocysts when flattened between slide and coverslip. The nematocysts were of a single type which did not conform clearly to any described for the family Proboscidactylidae (Russell, 1938; Hand, 1954; Calder, 1970). They appeared to be basatrichous haplonemes (Fig. 5). The nematocyst capsules left on severed pinnules and sabellid tube fragments appeared identical to those released from flattened planulae.

Behavior prior to attachment

Planulae that contacted severed *Schizobranchia* pinnules attached to the pinnules immediately. However, they often swam or crawled along paths that were almost, but not quite, tangential to severed pinnules without altering their direction or velocity as they passed the pinnules. Campbell (1968) observed that in the vicinity of an intact, extended sabellid, the currents passing through the crown of tentacular cirri greatly exceed the swimming velocity of *Proboscidactyla* planulae. My observations of planulae near severed pinnules and Campbell's result both suggest *Proboscidactyla* planulae take no active role in initiating contact with a suitable host.

Stimulus for attachment

To determine whether mechanical stimulation caused by contact with a ciliated surface might trigger nematocyst discharge and adhesion, a freshly excised portion of the branchial basket from a tunicate, *Chelyosoma productum,* and a piece of the lamellae from a scallop *Chlamys hastata*, were placed in each of 2 Syracuse dishes containing large numbers of planulae (about 250 in the first trial and 100 in the second). No planulae adhered to the ciliated ascidian or mollusc tissues. When severed *Schizobranchia* pinnules were added, planulae attached to the pinnules in large numbers. The presence of active cilia on a surface apparently does not, in itself, elicit nematocyst discharge.

Unattached planulae in crowded Syracuse dishes also did not adhere to fragments of *Schizobranchia* tube, although they frequently encountered the fragments. Such planulae failed to adhere even when squeezed lightly between 2 fragments of tube or a fragment of tube and the bottom of this dish. On the other hand, pieces of the collar folds, short lengths of contiguous body segments, and isolated portions of the ventral shields of *Schizobranchia* placed one at a time in Syracuse dishes containing planulae appeared to stimulate attachments as effectively as pinnules.

The great specificity of the attachment response suggest that a chemical stimulus found only on the body surfaces of sabellids is necessary to elicit nematocyst discharge in unattached *Proboscidactyla* planulae. I was unable to distinguish whether this chemical stimulus is an insoluble surface coating on the pinnules that the cnidoblasts detect only if they contact it directly, or a diffusable substance that triggers nematocyst discharge only in conjuction with a mechanical stimulus. Simple mechanical stimuli applied in the presence of mucus solutions or tissue "juices" from *Schizobranchia* failed to elicit a nematocyst response, but these solutions may have had toxic qualities that inhibited a nematocyst response.

Attachment to pinnules of a non-host sabellid species

Near Friday Harbor, *Schizobranchia insignis* is the most abundant sabellid species. *Eudistylia vancouveri* is morphologically similar to *Schizobranchia,* fairly common, and occurs in the same areas. However, *Eudistylia* tubes never bear *Proboscidactyla* colonies. Colonies can be successfully exchanged from one *Schizobranchia* specimen to another, but they regress when transplanted to *Eudistylia* (Strickland, 1971). Experiments comparing the tendencies of planulae to settle on *Schizobranchia* and *Eudistylia* pinnules revealed a clear preference for *Schizobranchia* although *Eudistylia* regularly stimulated attachment also (Fig. 6A and B). In A, the separate-dish design, 25 planulae and 10 *Schizobranchia* pinnules were placed in each of 4 culture dishes 2 cm in diameter. Four similar dishes were prepared with *Eudistylia,* rather than *Schizobranchia,* pinnules. In B, the competitive design, 25 planulae, 5 *Schizobranchia* pinnules, and 5 *Eudistylia* pinnules were placed together in each of 3 dishes. In both experiments the number of planulae that had attached to the *Schizobranchia* pinnules by 1, 2, 4, and 6 hr was significantly higher at the 99% confidence level (minimum value of t in Student test was 4.4 with 5 degrees of freedom). Nevertheless, in every trial or trial-pair some planulae attached to *Eudistylia* pinnules.

Elongation following attachment

Shortly after attaching to a pinnule, *Proboscidactyla* planulae lengthened along their longitudinal axes to a much greater extent than unattached planulae ever did

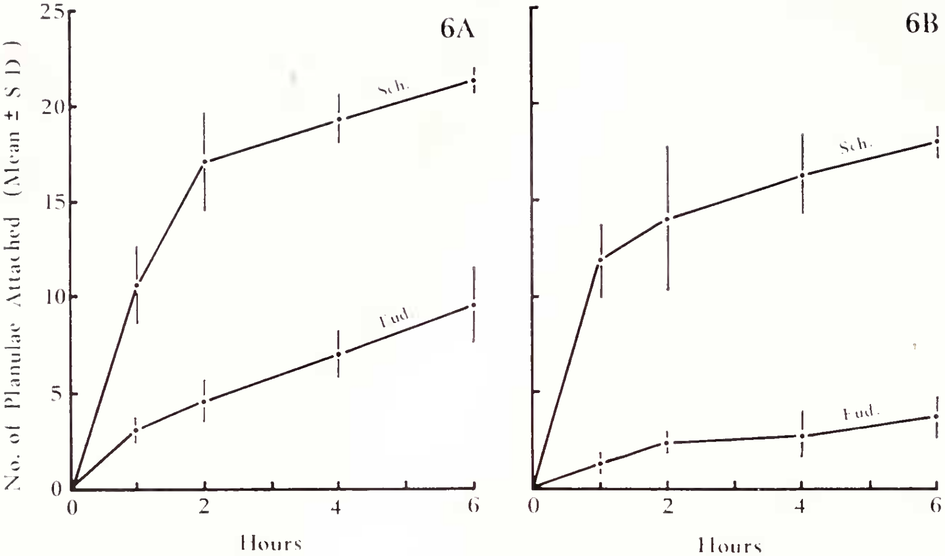
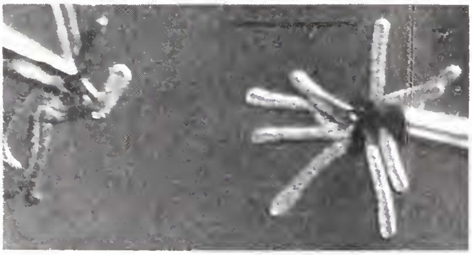


Figure 6. Experiments comparing planula settlement on pinnules from *Schizobranchia* and *Edistylia;* (A) separate dish design, (B) competitive design. Time elapsed following the addition of 25 planulae to each trial dish is plotted on the abscissas. The ordinates designate the mean number of planulae attached in all trials for each experimental design.

(Fig. 7). During elongation the cavity within the planula narrowed and sometimes nearly disappeared. Simultaneously the greatest diameter of the elongating planula shifted from anterior to posterior. The greater thickness of the posterior entoderm probably accounted for the posterior bulge of maximally elongated planulae (Fig. 7). The orientation of attachment (anterior, posterior, or lateral) had no visible effect on the shape of a planula upon elongation.

Data were obtained on the time between attachment and complete elongation for 25 planulae. Elongation required from 1.3 to 11 min ($\bar{x} = 4$ min, S.D. $= 2.7$).



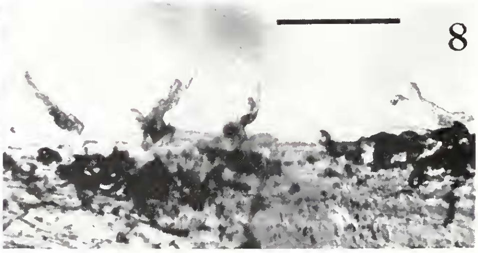


Figure 7. Elongated planulae after 12 hr adhesion to the fragment of tentacular cirrus held by the suction pipette on the right. The planula on the left had been attached for 1 min and had not yet elongated when the photograph was made; scale bar = 0.5 mm.

Figure 8. Newly metamorphosed *Proboscidactyla* polyps on the rim of a *Eudistylia* tube; scale bar = 0.5 mm.

The planulae that attached to severed *Eudistylia* pinnules during the inter-species comparison experiments (Fig. 6) elongated, but did so more slowly than planulae attached to *Schizobranchia* pinnules. Once elongated, attached planulae remained so in excess of 24 hr. By this time severed *Schizobranchia* pinnules had largely decomposed, although severed *Eudistylia* pinnules remained in good condition.

Planulae attached to the intact pinnules of a small *Schizobranchia* specimen (removed from its tube to prevent transfers to the tube rim) remained elongated in excess of 48 hr. These planulae and those that remained attached to pinnules instead of transferring to tubes never metamorphosed. Controls which completed their transfers almost always began metamorphosis within 12 hr. Elongation appeared to be associated exclusively with attachment to pinnules. Following transfer, planulae always rounded up within a few minutes. Transfer appears to initiate planula metamorphosis.

Desensitization to pinnules following attachment

Planulae swept into the crowns of intact sabellids only occasionally attached to more than one pinnule, although the curling and writhing of the worm's crown frequently brought the newly-attached planula into contact with several pinnules. Fifty-two planulae that had been attached to severed pinnules for 10–12 hr all failed to adhere when maneuvered into contact with freshly severed tentacular cirri from *Schizobranchia,* although 40 of them later transferred to tube fragments (Table 1). On 5 occasions individual planulae were touched with a second pinnule at 0.5 min intervals after attachment. Two planulae failed to adhere to the second pinnule on the first trial at 0.5 min. Two others adhered at 0.5 min and 1.0 min, but not at 1.5 min. None of these planulae had elongated appreciably before becoming desensitized to pinnule contacts. (About 1.3 min was the minimum time required to achieve full elongation in any of the 25 planulae timed). The fifth planula adhered to a proffered pinnule at 2.0 min, but not at 2.5 min. It required even longer, 9 min, to elongate and did not elongate completely. Thus desensitization occurs before elongation and the minimum time to desensitization is approximately 0.5 min.

TABLE I

Comparison of Schizobranchia *pinnules and tube surfaces as stimuli for the adhesion of attached planulae.*

Order of test surface application in each trial series	Number of planulae tested in each trial series (total 52)	Number of planulae adhering to each test surface (Total 40)				Number of planulae failing to adhere (total 12)
		pinnule	inside	mid-layer	outside	
pinnule, inside, outside	30	0	5		18	7
pinnule, outside, inside	9	0	0		7	2
pinnule, mid-layer, outside	3	0		0	2	1
pinnule, outside, mid-layer	10	0		1	7	2

Twenty-one planulae pulled off pinnules after 10–12 hr of attachment shortened up and resumed swimming after approximately 5 min. Within 10 min all of these planulae had recovered the ability to attach to *Schizobranchia* pinnules. Pinnule contact apparently must be maintained to prevent planulae from discharging nematocysts in response to new pinnule contacts.

Acquisition of a nematocyst response to worm tube

After becoming desensitized to pinnule contacts, attached *Proboscidactyla* planulae eventually begin to adhere when brought into contact with sabellid tube material. This change in effective stimulus for nematocyst discharge will be termed respecification. Under natural conditions attached planulae can only contact worm tube when the worm withdraws its crown of tentacular cirri. To estimate the time required for a newly attached planula to become responsive to worm tube I touched individual planulae to fragments of worm tube at intervals ranging from 1 min to 45 min after attachment. Out of a total of 20 transfers, the 2 earliest occurred 4 and 6 min after attachment.

An attempt to obtain a more accurate estimate of the time required for respecification was made by touching individual planulae to worm tube fragments at 2 min intervals, starting 2 min after attachment. However, the planulae subjected to these manipulations usually came off their pinnules or failed to adhere to the tube fragment within 30 min. Table II displays data from the 6 trials in which planulae adhered to tube fragments. Some of the first adhesions were not tenacious enough to result in a transfer, but eventually 5 out of the 6 planulae transferred. The one exception was injured accidentally before its 10 min trial. None of these planulae discharged nematocysts until they had been attached for at least 6 min. All 6 planulae had been elongated for at least 3 min before first adhering to a worm tube.

These and other observations suggested that elongation was associated with, and ordinarily preceded, respecification. However, 4 planulae that were substantially less than fully elongated nevertheless transferred successfully. Respecification and elongation may begin with the same stimulus or depend upon a common physiological event, but complete elongation is not a prerequisite for transfer.

Table II

Time requirement for respecification.

Elapsed time between attachment and elongation of each of 6 planulae (min)	Results of trials on tube at 2 min intervals (min after attachment)	
	Adhesion without transfer	Adhesion followed by transfer
2	6	8
2.5	8, 10, 12	18
11		14
3.5	8	
1.5		12
2.5		6

Orientation of attachment and transfer

In many, but not all, of the observed attachments, a point at or to one side of the anterior end of the planula adhered to the pinnule. However, by using a manipulator to maneuver the severed pinnules posterior attachments were readily obtained. Promptly after contact, planulae attached by the pointed posterior end often toppled over and adhered by one side, which suggests that physical instability may account for the comparative rarity of posterior attachments. Planulae that remained attached by the posterior and elongated normally, the enlarged end being the posterior as usual. On 6 occasions I noticed elongated planulae that had attached by their posterior ends after being swept into the plumes of intact sabellids.

Although many planulae, having attached by their anterior ends, adhered by their posterior ends during transfer, again this was not always the case. Often they adhered to worm tube fragments by one side. Four planulae, having attached to pinnules by their posterior ends, subsequently adhered to tube fragments by their anterior ends and transferred. The absence of a requirement for a particular orientation during either elongation or transfer suggests either that two populations of nematocysts are intermingled, or that nematocysts from all parts of the epidermis are functionally identical.

Stimulus for transfer

The data presented in Table I suggest that the outside of *Schizobranchia* tubes stimulates transfer far more effectively than does the inside or a middle layer. In obtaining these results the responsiveness of each attached planula to pinnule contacts was first tested by touching it to a short section of isolated *Schizobranchia* tentacular cirrus. Having obtained a negative response, the planula was then touched to either the inner surface of a *Schizobranchia* tube fragment or a middle layer of a "peeled" tube fragment. If the planula failed to transfer it was touched to the outer surface of another fragment of the same tube. With other planulae the same stimuli was applied in reverse order.

To determine whether attached and respecified *Proboscidactyla* planulae might adhere relatively non-selectively, 3 non-sabellid substrates from the mooring float community were tested: the tunic of *Cheliosoma productum*, test of the ectoproct *Membranipora tuberculata,* and an empty barnacle shell removed from the outside of a sabellid tube.

None of the 5 planulae tested on each of the 3 non-sabellid substrates adhered, although all 15 subsequently transferred when touched to a fragment of *Schizobranchia* tube. The stimulus for transfer, whether a film of microorganisms or not, appeared to be exclusively a property of sabellid tube material.

Individual planulae successfully transferred to fragments of *Eudistylia* tube on numerous occasions, sometimes after attachment to severed *Eudistylia* pinnules. The behavior of planulae that attached to the pinnules of small intact specimens of *Eudistylia* was indistinguishable from that of control planulae on *Schizobranchia;* they elongated, transferred, and metamorphosed into minute one-tentacled polyps (Fig. 8). Clearly *Eudistylia,* although not a host for *Proboscidactyla,* can induce

Proboscidactyla planulae to settle whereas other surfaces found in the same localities cannot.

DISCUSSION

In comparative settling experiments, *Schizobranchia* pinnules were preferred to *Eudistylia* pinnules, but *Proboscidactyla* planulae attached to pinnules of both sabellid species. Once attached, the responses of planulae to *Eudistylia* were qualitatively indistinguishable from the responses elicited by *Schizobranchia*. None of the other test substrates induced planulae to adhere even momentarily. Planulae metamorphosed on intact specimens of *Eudistylia* in the laboratory and there is no reason to suspect that they fail to do so in the field. Apparently the deficiencies of *Eudistylia* as a host for *Proboscidactyla* are not manifested until after metamorphosis.

Nematocyst responses play a central role in the settlement of *Proboscidactyla* planulae and constitute a major part of the behavioral repertoire of these larvae. Free-swimming planulae ordinarily discharge nematocysts only upon contact with the pinnules of a sabellid. Contact with non-sabellid, ciliated surfaces does not elicit nematocyst discharge, although the mechanical stimulus is probably comparable to that provided by sabellid pinnules. However, contact with any body surface of *Schizobranchia* results in attachment. *Eudistylia,* although closely related to *Schizobranchia* and morphologically very similar, is less effective in stimulating planulae to attach. Following attachment and respecification, planulae again respond specifically, this time discharging nematocysts upon contact with the outer surfaces of sabellid tubes. These results suggest that specific chemical stimuli are needed to elicit nematocyst discharge in *Proboscidactyla* planulae.

Planulae discharge nematocysts individually at sites of contact rather than en masse. This indicates either that direct contact with a chemically stimulating surface is required to excite a cnidoblast, or that mechanical as well as chemical stimulation is needed. The first possibility has never been described, but the second, dual stimulation, has been demonstrated in some cnidarians by applying chemical and mechanical stimuli separately and in combination (Pantin, 1942; Jones, 1947; Burnett, Lentz, and Warren, 1960). I was unable to excite the nematocysts of *Proboscidactyla* planulae with simple mechanical stimuli in the presence of mucus solutions or tissue "juices" from *Schizobranchia*. Therefore it is conceivable that contact chemoreception alone mediates the nematocyst response in this case, although these negative results do not constitute a conclusive demonstration.

After about 30 sec of attachment to a pinnule, a *Proboscidactyla* planula becomes desensitized to additional pinnule contacts. Subsequently, the nematocyst response is respecified, sabellid tube replacing pinnule as the effective stimulus. Intercellular controls of nematocyst function must be postulated to explain desensitization and respecification. There may be two functional classes of nematocysts, one responsive to pinnule and the other to worm tube. Because any part of a planula can adhere to either pinnule or worm tube, it follows that if two types of nematocysts exist, they must both be distributed uniformly over the epidermal surface. Prior to attachment, the pinnule nematocysts would be ready to discharge while the tube nematocysts would be inhibited. After attachment, owing to changes in physiological state throughout the cnidoblast population, the tube nematocysts would become readied and the pinnule nematocysts inhibited. Alternatively, there may be only one type of nematocyst in *Proboscidactyla* planulae. Physiological events associated with attachments to a pinnule would respecify the remaining cnidoblasts to discharge only to worm tube.

In the nematocyt literature the term "independent effector" has been used in different ways. Early authors used the term specifically to indicate that nematocysts are not directly excited by the nervous system (Parker and Van Alstyne, 1932; Pantin, 1942; Jones, 1947). More recently authors have described examples of endogenous nematocyst controls operating through unidentified physiological pathways as evidence against the independent effector hypothesis (Davenport, Ross, and Sutton, 1961; Ross and Sutton, 1964; Sandberg, Kanciruk, and Mariscal, 1971; Oshida, 1972). It is possible that the nematocysts of *Proboscidactyla* planulae are independent effectors in the original restricted sense, although their function is clearly subject to endogenous controls.

Although innervation of some cnidoblasts has been histologically demonstrated (Westfall, 1970; Westfall, 1971), the settlement behavior of *Proboscidactyla* planulae can be explained without assuming that such innervation exists. Desensitization probably requires a minimum of about 30 seconds to complete and sometimes takes over 2 minutes. Respecification requires several minutes. Nervous (or epithelial) conduction would transmit the message of attachment from one end of the 250 μ planula to the other in a few milliseconds. If nervous conduction is involved, there presumably are slow steps at the receptor sites, cnidoblasts, or both to account for the observed delays. On the other hand, slow conveyance of information by a non-nervous process might largely account for the considerable time lag before desensitization and, in combination with a slow step in the cnidoblasts, for the still greater delay prior to respecification. Both desensitization and respecification are reversible changes maintained only by continuous contact with a sabellid pinnule. This suggests that information is continuously transferred from the attachment site. It is possible that a metabolite diffuses from the attachment site through the tissues of the planula and triggers the sequence of events that follow attachment.

Planulae that attached and did not transfer remained elongated for extended periods of time, but never metamorphosed. After transferring to the rims of sabellid tubes, planulae that had previously been attached to pinnules promptly rounded up and subsequently commenced metamorphosis. These observations indicate that the stimulus for metamorphosis is not the same as the stimulus for attachment, desensitization, elongation, or respecification. The stimulus that initiates metamorphosis and the stimulus for adhesion and transfer to sabellid tube could be one and the same. Elongation, while not a prerequisite for transfer, may be a behavioral adaptation that increases the probability of transfer by increasing the likelihood of contact with the sabellid tube rim.

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SUMMARY

Planulae of the symbiotic hydroid *Proboscidactyla flavicirrata* settle on the rims of sabellid tubes by adhering sequentially and specifically to two different substrates. For both steps, nematocysts are the agents of adhesion. Although the cnidoblasts of these planulae require local excitation, they are subject to endogenous controls.

Upon being swept into the plumes of tentacular cirri that sabellids extend from their tubes, planulae attach to individual pinnules (branches of the tentacular cirri) by discharging nematocysts. Within 2 min following attachment, the planulae cease discharging nematocysts in response to additional pinnule contacts. Planulae transfer to the rims of sabellid tubes by adhering with nematocysts when the sabellids retract their plumes. Cnidoblasts of planulae only become responsive to contact with sabellid tube after 4 min or more of continuous attachment to pinnules. Transfer initiates metamorphosis.

Planulae are capable of settling and metamorphosing on *Eudistylia vancouveri*, a sabellid species that is sympatric with the normal hosts of *Proboscidactyla*, but will not support colonies. Apparently the deficiencies of *Eudistylia* as a host are manifested only after planula metamorphosis.

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NOTE ADDED IN PROOF

The identification of the planula nematocysts given in this report is in error. They are microbasic euryteles not basitrichs.